CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN

Number 70 October, 1954

EXPERIMENTAL EVIDENCE OF REPRODUCTIVE ISOLATION BETWEEN TWO SUBSPECIES OF PEROMYSCUS MANICULATUS

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Accepted for publication May 1, 1954.

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INTRODUCTION

THE development and persistence of genetic differences between species of animals occur only with isolation of breeding populations. Experimental study of isolating mechanisms reveals something of the processes of evolutionary development by suggesting factors which have brought about the present differentiation and distribution of animal groups. Such studies may also aid in predicting the course of future development of animal populations.

Reproductive isolation between population groups in mammals may be achieved by various mechanisms. Under experimental conditions sexual isolation was found by Blair and Howard (1944) to be present between species belonging to the Peromyscus maniculatus species group. Blair (1953) reported that mice of the sympatric species Peromyscus truei and P. nasutus discriminate between members of their own and the other species. Liu (1953a) discovered that hybrids of certain subspecies in the P. maniculatus species group were similar in fertility to both parent stocks, but that average fertility was reduced in interspecific crosses. This reduction of fertility in interspecific crosses

he found to be due to the fertilization of fewer of the liberated ova in the pregnant female and to an increase in the proportion of dead fetuses (Liu, 1953b).

In the present study an attempt has been made to ascertain if assortative mating (the selection of certain types of mates) and sexual isolation exist between two subspecies of Peromyscus maniculatus. The classification of isolating mechanisms given by Dobzhansky (1941: 257) will be followed.

Acknowledgments

I wish to express my appreciation to Lee R. Dice for valuable advice in the planning and execution of this study. I am indebted to Charles W. Cotterman and Philip J. Clark for material aid in the statistical analysis. Lee R. Dice and Philip J. Clark read the manuscript. The Laboratory of Vertebrate Biology, University of Michigan, supported the study.

METHODS AND MATERIALS

The methods employed in this study are somewhat similar to those developed by Blair and Howard (1944). Different kinds of mice were placed together in laboratory cages to form an artificial society wherein it was possible for each mouse to associate with others or to remain alone.

Experimental Conditions

An artificial society was composed of a pair of mice of one kind and a female of another kind. Each society was housed in three wire-screen cages which were connected by wooden tunnels. Each mouse in a society thus had access to any cage. The tunnels were provided with metal drop gates so that the cages could be isolated to facilitate observation. Each cage had a floor space of 9 by 16 inches, and each was provided with food, water, nest box, and nesting material.

The cages were arranged on the shelves of a rack in a corner of the laboratory with a southern and an eastern exposure. During the late winter, when the experiments were begun, the temperature of the room was kept at approximately 72°F., but during the summer the room temperature could not be completely controlled and occasionally reached higher levels.

EXPERIMENTAL PROCEDURE

Only healthy mice of breeding age were used in the experiments. Almost all of the mice tested were sexually active, as was ascertained

from the condition of the external genitalia. As far as could be learned from laboratory records of matings and litters, none of the mice combined to form any particular artificial society had been previously associated in cages with others of that society.

At the beginning of an experiment a mouse was placed in each of the three connected cages. The mice were then allowed to move freely about in the cages. Bright lights were turned on over the cages each morning to ensure the onset of the inactive period of the mice, which coincides with daylight. After the mice became inactive, almost always between 8:00 and 10:00 A. M., the drop gates were closed, and the groups that had been formed were recorded. The mice were also inspected for evidence of fighting. Food and water dishes were replenished, and the drop gates were opened for the remainder of the day and the following night.

Occasionally, the mice were reluctant to settle down, or movement of the animals was observed to occur just before the gates were closed. The records for these days were not included in the analysis of the data.

Each experiment continued for approximately 33 days, a period equal to one and one-half times the average gestation period of the mice, unless it was terminated earlier by the birth of a litter. Usually, a female with a litter remained separate from the other mice, and groups formed on the day the litter was discovered were not included in the data. After an experiment was terminated the females in the society were isolated for a month to ascertain if they were pregnant.

The data obtained are of three kinds: (1) records of the association of the mice with each other, (2) records of the number of homogamous and hybrid litters produced, and (3) records of fighting among the mice.

At the time when observations were made on any one day the three mice could occur in any one of five types of groups: (1) All three mice might be together in the same cage. As a result of random association, a group of three would occur on one-ninth of the days. (2) Each mouse might occupy a different cage. This distribution would occur by chance in two-ninths of the observations. (3) The male and female of one kind of mouse might occupy one cage, while the female of the other kind remained in a different cage– " like pairs." (4) The male of one kind and the female of the other kind might be found together in a particular cage to the exclusion of the other female– " unlike pairs." (5) The two females might associate in one cage with the male in a separate cage– " female pairs." Each of these types of pairs, groups 3, 4, and 5, could occur at random on two-ninths of the days.

Two or more individuals were regarded as associated when they occurred in the same cage. Occasionally, evidence of separation was noted within a cage. For example, three mice might occur together in one cage, with two of them occupying the nest box while the third remained in a corner of the cage. This situation, however, was recorded as a group of three. The status of within-cage groupings was rarely clear and, therefore, has not been subjected to analysis.

The data derived from the groups formed by the mice were analyzed

by the chi-square method, which tested the observed number of times the various groups were formed against the number of times they would occur if the mice had associated at random.

Litters produced in the artificial society could always be associated with the female which bore them. Even if the young were deserted at the time the observations were made, the previous pregnant condition would have been noted. Since only one male occurred in the artificial society, there was no doubt as to the paternity of the litter.

It was impractical to watch the mice for various periods during the day or night. The records of fighting, therefore, depended on circumstantial evidence. Scratches, especially on the head and tail, and an ungroomed condition were considered indicative of fighting.

Experimental Animals

The artificial societies in these experiments were composed of two subspecies of Peromyscus maniculatus: P. m. bairdi and P. m. gracilis. The laboratory stock of bairdi, Washtenaw, originated from individuals caught in 1946 and 1947 in fields near Ann Arbor, Michigan. The animals tested were from the first and subsequent laboratory-bred generations.

The laboratory stock of gracilis, Pine Lake, was reared from individuals taken by W. F. Blair from the Cusino Wildlife Refuge, Munising, Michigan, in 1940. I added a few females to this stock from another location in the Cusino Wildlife Refuge in 1947. One female gracilis, in experiment 115, was a field-caught individual from this latter location. Mice from the sixth and subsequent laboratory-bred generations were used in the experiments other than No. 115.

Gracilis and bairdi are members of an interbreeding chain of closely related species. The two races will cross in the laboratory, and they produce fertile offspring (Dice, 1931), but they do not do so readily.

EXPERIMENTAL RESULTS

Eighteen experiments were conducted between February and May, 1949, and 12 between April and July, 1952. Fifteen of these 30 experiments (nine in 1949 and six in 1952) were devoted to artificial societies, each composed of a male gracilis, a female gracilis, and a female bairdi. In the remaining 15 experiments each artificial society was composed of a male bairdi, a female bairdi, and a female gracilis. For convenience the two series of experiments will be called, respectively, the male gracilis series and the male bairdi series.

The 1952 experiments were compared with the 1949 experiments by means of the contingency chi-square test. The groups formed by the mice in 1952 differed significantly from those formed in 1949. For the male gracilis series of experiments the chi-square value of this differ-

ence is 10.16 (with four degrees of freedom), and the one for the male bairdi series is 29.95 (with four degrees of freedom). The reason for this difference in group formation between the two years was not ascertained.

The chief difference in pattern of group formation between the experiments of 1949 and 1952 appears to be one of degree rather than of kind. The group type most often formed by the mice in the 1949 experiments was even more characteristic in the 1952 experiments. Since this trend in group formation by the mice was very apparent in both years and was characterized by very high chi-square values, as noted below, the experiments conducted in the two years were combined for further analysis.

Artificial societies composed entirely of bairdi or of gracilis individuals were not studied. Experience at the Laboratory of Vertebrate Biology, however, indicates that laboratory-bred individuals of gracilis and of bairdi are very social among their own kind. The social tendency of bairdi was very apparent in an experimental population studied by F. E. Smith at the Laboratory.

Artificial Societies of Gracilis Males with Gracilis and Bairdi Females

The data obtained from the 15 experiments of the male gracilis series are given in Table I, which shows that in each experiment, except No. 116, the group of three mice together was formed more often than any other group. In order to test for heterogeneity among the experiments, the significance of the difference between the observed groupings and those which would be expected under conditions of randomness was tested for each experiment by chi-square. The expected frequencies of the five groups shown in Table I were too small to permit effective use of chi-square on all the groups. For this reason arbitrary combinations of groups " a" and " b" and of groups " c," " d," and " e" (Table I) were made so that a chi-square with one degree of freedom was obtained for each experiment. As can be seen from Table I, in most experiments the groupings were significantly nonrandom; however, the various experiments failed to agree in the extent of their departure from randomness, as the heterogeneity chi-square was significant at the 1 per cent level.

The total observations in each group type for all 15 experiments are given at the bottom of Table I, together with the expected values based on random association of the mice. The group of three mice was observed more frequently than expected; the other four groups occurred less frequently than expected. The pooled chi-square, calculated from the data obtained by combining the 15 experiments, for deviation from random grouping is 1353.27 (with four degrees of freedom). The probability of obtaining a higher chi-square value is much less than one in one hundred.

TABLE I

Social Groups Formed in an Artificial Society Composed of One Male Peromyscus maniculatus gracilis, One Female P. m. gracilis, and One Female P. m. bairdi

Experiment Number	Groups a	b	c	d	e	Total Observations	Chi-Square Value[2]	df	Number of Days	Offspring g x g	Offspring b x g	Most Frequent Association
	$\frac{g♂:g♀}{b♀}$[1]	$\frac{g♂:b♀}{g♀}$	$\frac{g♀:b♀}{g♂}$	$\frac{g♂:g♀:b♀}{\text{together}}$	$\frac{g♂}{\frac{g♀}{b♀}}$							
103	1	3	1	18	0	23	6.82	1	25		x	All together
104	2	1	4	26	0	33	16.71	1	35			All together
107	6	5	1	11	0	23	.11	1	27	x		All together, like pairs, or unlike pairs
109	6	6	3	18	1	34	1.15	1	37			All together. ♀g not in estrus
111	2	3	2	26	0	33	11.47	1	41			All together. ♀g not in estrus
113	3	1	2	27	0	33	13.96	1	38			All together. ♀g not in estrus
116	13	3	6	7	3	32	.40	1	34	x		Like pairs
118	4	3	3	14	1	25	2.74	1	31	x	x	All together
119	11	1	2	18	1	33	.87	1	42			All together or like pairs
122	1	4	6	14	0	25	6.05	1	27	x		All together
124	2	0	2	28	1	33	19.69	1	35			All together
126	4	8	3	21	0	36	1.80	1	36			All together
128	3	0	0	29	0	32	15.94	1	34			All together
130	3	0	3	27	0	33	16.71	1	35			All together
132	3	4	10	14	2	33	7.21	1	34			All together or female pairs. ♀g nose scratched late in experiment
Totals												
Expected	64	42	48	298	9	461				4	2	
Values	102.44	102.44	102.44	51.22	102.44	460.98						

[1] g = P. m. gracilis; b = P. m. bairdi. Mice above horizontal line were in a different cage from mice below.

[2] The chi-squares were computed after combining groups a and b and groups c, d, and e.

Analysis of Chi-square

Item	Chi-square	d.f.	P.
Total	121.63	15	<.01
Deviation	85.91	1	<.01
Heterogeneity	35.72	14	<.01

Of especial interest in the pooled data is the comparison of " like pairs" with " unlike pairs," which have equal probabilities of occurring at random. The chi-square value for this comparison, 4.56 (with one degree of freedom), has a probability of approximately .04, " like pairs" occurring more often than expected. The fact that the experiments are significantly heterogeneous, however, prevents one from asserting that all of the males prefer their own type of female to a female of the other type, although it is apparent that some of them do.

As noted in Table I, there was only one indication, in experiment 132, that fighting occurred among the mice tested. Hence, the associations or exclusions of mice in the groups were not attended by fighting that resulted in wounds or other visible signs.

Artificial Societies of Bairdi Males with Bairdi and Gracilis Females

The associations formed by the mice in 15 experiments of the male bairdi series, together with other data, are recorded in Table II. In 12 of the experiments all three mice were associated for most of the daily observations. " Like pairs" were formed in experiments 108 and 112, and "female pairs" were formed as often as groups of three in experiment 114. As with the male gracilis experiments, chi-square tests were applied to the individual experiments after the first two and the last three groups were arbitrarily pooled into two combinations. Most of the experiments differed significantly from random expectation. The heterogeneity chi-square, however, was significant at the 1 per cent level, so that the behavior of the mice in the different experiments is far from consistent.

For the group of three mice the total observations for the 15 experiments exceed the expected value, but in each of the other groups the observed values are less than the expected values. The pooled chi-square for deviation of observed values from expected values is 1188.99 (with four degrees of freedom). The probability of this chi-square is much less than 0.01.

When the observed totals for like pairs and unlike pairs are compared with the expected numbers, which are the same for the two groups, a chi-square of 13.46 (with one degree of freedom) is obtained. There is a strong tendency for some males to prefer females of their own kind to those of the other type. The heterogeneity between experiments, however, prevents one from attributing this tendency to all of the males.

There was evidence of fighting in only one experiment of the male bairdi series. A female gracilis in experiment 127 was observed with pelage disarranged on one day; otherwise, to all appearances, the mice lived amicably together.

TABLE II

Social Groups Formed in an Artificial Society Composed of One Male Peromyscus maniculatus bairdi, One Female P.m. bairdi, and One Female P.m. gracilis

Experiment Number	Groups a	b	c	d	e	Total Observations	Chi-Square Value[2]	d.f.	Number of Days	Offspring b x b	Offspring g x b	Most Frequent Association
	$\frac{b\sigma^{\prime}:b\varphi}{g\varphi}$[1]	$\frac{b\sigma^{\prime}:g\varphi}{b\varphi}$	$\frac{b\varphi:g\varphi}{b\sigma^{\prime}}$	$\frac{b\sigma^{\prime}:b\varphi:g\varphi}{\text{together}}$	$\frac{b\varphi}{\frac{b\varphi}{g\varphi}}$							
105	2	8	3	19	1	33	2.67	1	36			All together or unlike pairs
106	4	1	0	27	1	33	11.47	1	36			All together. ♀g not in estrus
108	10	6	0	6	1	23	5.88	1	27	x		Like pairs
110	4	0	2	14	0	20	4.84	1	24	x		All together
112	19	0	0	8	1	28	6.22	1	30		x	Like pairs or all together
114	8	2	12	11	0	33	2.67	1	38			Female pairs or all together
115	6	1	1	24	0	32	6.60	1	37			All together
117	5	5	3	14	0	27	.60	1	29	x		All together
120	5	4	1	7	1	18	.23	1	22	x	x	Like pairs, unlike pairs, or all together
121	0	3	3	21	0	27	12.15	1	29	x		All together
123	1	0	2	30	0	33	22.92	1	36	x		All together
125	3	1	0	18	0	22	6.15	1	23	x	x	All together
127	3	4	5	19	2	33	7.21	1	35	x		All together. ♀g not in estrus
129	6	2	9	13	2	32	4.90	1	38			All together or female pairs
131	0	0	0	29	0	29	23.20	1	31	x	x	All together
Totals Expected	76	37	41	260	9	423				9	4	
Values	94	94	94	47	94	423						

[1] g = P. m. gracilis, b = P. m. bairdi. Mice above horizontal line were in a different cage from mice below.

[2] The chi-squares were computed after combining groups a and b and groups c, d, and e.

Analysis of chi-square

Item	Chi-square	d.f.	P.
Total	117.71	15	<.01
Deviation	53.86	1	<.01
Heterogeneity	63.85	14	<.01

Reproductive Isolation

Nineteen litters of young were produced in 15 of the 30 experiments (Tables I and II). Four litters were produced by gracilis parents and nine by bairdi parents. Two litters were from bairdi x gracilis crosses, and four litters were from gracilis x bairdi crosses. From these data the probabilities of individual fertility for the two subspecies were calculated by use of the formula derived by Liu (1953a). The probability of an individual gracilis being fertile in these experiments is 0.516 and of an individual bairdi is 0.775. From these probabilities reproductive isolation indices (Liu, 1953a) of 0.20 for gracilis x bairdi crosses, 0.50 for bairdi x gracilis crosses, and 0.33 for the reciprocal crosses are obtained. The isolation index varies between +1, indicating complete isolation, and -1, indicating complete cross-mating in preference to mating of likes.

Table III gives the chi-square values of the isolation indices. The chi-square value of the isolation index of bairdi x gracilis crosses is statistically significant at the 5 per cent level. For gracilis x bairdi crosses the value is not statistically significant, but for both reciprocal crosses the value is again significant at the 5 per cent level. Analysis of chi-square discloses no significant heterogeneity between the two crosses. These calculations indicate that some reproductive isolation exists between bairdi and gracilis.

TABLE III

Chi-square Test for Reproductive Isolation in Crosses Between Peromyscus maniculatus gracilis and P. m. bairdi

Matings	Fertile Matings	Sterile Matings	Total	Chi-Square	d.f.	P.
bairdi x gracilis	observed 2	13	15	4.44	1	0.05-0.02
	expected 6	9	15			
gracilis x bairdi	observed 4	11	15	1.11	1	0.30-0.20
	expected 6	9	15			
Both reciprocal crosses	observed 6	24	30	5.00	1	0.05-0.02
	expected 12	18	30			

Analysis of Chi-square

Item	Chi-square	d.f.	P.
Total	5.55	2	0.02-0.01
Deviation	5.00	1	0.05-0.02
Heterogeneity	0.55	1	0.90-0.80

DISCUSSION

One may conclude from the data presented that in artificial mixed societies the subspecies bairdi and gracilis are highly social and live together in mixed aggregations even when they have the opportunity to nest separately. Though variation occurred among replicate experiments, the tendency for all three mice to nest together in almost all of the experiments was outstanding. In only four of the 30 experiments (Nos. 108, 112, 114, 116) were definite pairs maintained, as indicated by the groups found during daylight hours.

A further evidence of the sociability of these mice in artificial societies is the absence of evidence of fighting. On one occasion in each of two experiments fighting may possibly have occurred. It is possible that fighting would have been somewhat more common and that social dominance would have been demonstrated if the artificial societies had each contained two males.

The social tendency of mice of the genus Peromyscus is also indicated by field records. Howard (1949) reported occasional mixed aggregations of P. m. bairdi and P. leucopus noveboracensis during winter in nest boxes placed in the ground near the edge of a woods. Close association between individuals of other kinds of small mammals in California is suggested by the data of Evans and Holdenried (1943). In 88 double captures there were 25 instances with evidence of fighting. Such evidence, however, was noted in only one instance of ten captures in which different species of Peromyscus were taken together.

In my experiments the groups formed by the mice before a female became pregnant were compared by means of the contingency chi-square with the groups formed after a female became pregnant. For each series of experiments the pooled chi-square value was not significant statistically. Thus, pregnancy of one of the females did not change the pattern of group formation in the artificial societies.

The data in these experiments give some evidence for assortative association and for sexual isolation between gracilis and bairdi.

Some reproductive isolation also exists, as shown by the measurements of fertility, from which the isolation indices were derived. Several isolating mechanisms that prevent hybridization or the development of hybrids are listed by Dobzhansky (1941). The tests used here do not indicate which of these mechanisms operate between gracilis and bairdi.

An interesting comparison may be made at this point. Reproductive isolation between bairdi and blandus is negligible (Liu, 1953a), and intermediate, interbreeding populations between the two subspecies are known (Osgood, 1909). On the other hand, bairdi and gracilis form opposite ends of a chain of interbreeding subspecies (Osgood, 1909), and, as will be shown, intermediate forms are not known. Bairdi and blandus are small-footed, short-tailed forms, presumably adapted to relatively open habitats; gracilis is a large-footed, long-tailed form, adapted to a forest habitat (Horner, 1954). Morphological differentiation

between bairdi and gracilis has progressed further than between bairdi and blandus, and this appears to be paralleled by the degree of reproductive isolation achieved.

Since my evidence indicates that reproductive isolation is not complete and that the two forms will live together under laboratory conditions, it would seem that, if the ranges of bairdi and gracilis were to overlap, some hybridization would occur. Because of clearing of the forest and cultivation of the land, bairdi has extended its range and occupies the same region with gracilis in Charlevoix and Menominee counties, Michigan (Dice, 1931; Hooper, 1942). No intergrades have been found in nature, however, probably because of their rather strict ecological separation (Osgood, 1909; Dice, 1931; Hooper, 1942). It has been shown experimentally that the habitat preferences of these two subspecies are undoubtedly genetic (Harris, 1952).

Apparently, then, genetic differences gradually accumulated between gracilis and bairdi during geographic isolation. This divergence resulted in adaptation to different habitats and in partial development of mechanisms which exclude hybridization or which possibly may arrest the development of hybrid offspring. One or more of these partly developed isolating mechanisms, together with ecological isolation, would presumably be sufficient to prevent the interbreeding of gracilis and bairdi populations in nature.

SUMMARY

Assortative mating and reproductive isolation between Peromyscus maniculatus bairdi and P.m. gracilis were studied in artificial societies in the laboratory. The societies were composed of a male and a female gracilis and a female bairdi in each of 15 experiments, and of a male and a female bairdi and a female gracilis in each of 15 additional experiments.

All mice showed a strong tendency to nest together during the daytime in each series of experiments. The deviations of the observed associations of the mice from the expected random associations were significant at the 1 per cent level. There was a tendency for males and females of the same subspecies to associate more often than males and females of different subspecies.

A degree of reproductive isolation, in the form of mechanisms which hinder cross-mating or which arrest the development of hybrid offspring, is shown to exist between gracilis and bairdi. The reproductive isolation index for gracilis x bairdi crosses was 0.20, for bairdi x gracilis crosses was 0.50, and for the reciprocal crosses was 0.33. The last two values are significant at the 5 per cent level.

The development of isolating mechanisms, which in nature prevent effective hybridization, and also the development of different habitat preferences presumably occurred at a time when bairdi and gracilis were completely isolated geographically. These several reproductive

isolating mechanisms are effective in preventing intergradation now that the two subspecies have subsequently come into contact over a limited part of their ranges.

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